Effect of timber harvesting on microbial biomass fluxes in a northern Rocky Mountain forest soil[1]

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Microbial biomass and relative bacterial and fungal percentages were measured in organic forest soil from a Rocky Mountain site subjected to four harvesting treatments: RL, clear-cut and residue left; RR, clear-cut and residue removed; RB, clear-cut and residue burned; C, uncut control. Microbial biomass peaked in spring and fall regardless of treatment. Biomass in soil from the RB treatment was significantly ($p < 0.05$) less than that in soil from the other treatments most of the year; biomass did not significantly differ in soil from the RR and C treatments. During summer and winter, microbial biomass in soil from the RL treatment was significantly greater than that in soil from any other treatment, probably because of the large amount of organic residue left after harvest; moreover, this residue insulated the soil, preventing it from drying or freezing. At soil temperatures above 5°C, microbial biomass correlated positively with soil moisture regardless of treatment; at soil temperatures below 2.5°C, microbial biomass correlated positively with increasing soil temperature. During periods with snow cover, bacterial and fungal percentages were roughly equal regardless of treatment; during the rest of the year, bacterial percentages were high in the RL and RB treatments and low in the RR and C treatments. During periods without snow cover, bacterial and fungal percentages correlated positively with increasing soil pH; however, at near-freezing temperatures the percentage of bacteria and fungi seemed unaffected by soil pH. These findings suggest that treatments that remove a large portion of available site nutrients while reducing soil microbial activity could limit stand development.

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La biomasse microbienne et les pourcentages relatifs de bactéries et de champignons ont été mesurés dans les horizons organiques d'un sol d'une station des montagnes Rocheuses soumise à quatre méthodes de récolte: RL, coupe à blanc et résidus laissés sur place; RR, coupe à blanc et résidus enlevés; RB, coupe à blanc et résidus brûlés; C, témoin non coupé. La biomasse microbienne a atteint un maximum au printemps et à l'automne sans égard au traitement. La biomasse du sol pour le traitement RB était significativement inférieure ($p < 0,05$) à celle observée pour les autres traitements pendant presque toute l'année; la biomasse dans le sol n'a pas varié significativement pour les traitements RR et C. Durant l'été et l'hiver, la biomasse microbienne du sol pour le traitement RL était significativement plus grande que la biomasse du sol de n'importe quel autre traitement, probablement à cause de la grande quantité de résidus organiques laissés après la récolte; d'ailleurs ces résidus ont isolé le sol, le préservant contre la dessication ou le gel. Pour les températures du sol supérieures à 5°C, la biomasse microbienne était correlée positivement avec la température du sol sans égard au traitement; à des températures du sol inférieures à 2,5°C, la biomasse microbienne était correlée positivement avec l'accroissement de la température du sol. Durant les périodes avec une couverture de neige, les pourcentages bactériens et fongiques étaient sensiblement égaux sans égard au traitement; durant le reste de l'année, les pourcentages bactériens étaient élevés dans les traitements RL et RB et bas dans les traitements RR et C. Durant les périodes sans couverture de neige, les pourcentages bactériens et fongiques étaient corrélés positivement avec l'accroissement du pH du sol mais pour les températures près du point de congélation, ces pourcentages ont semblé non affectés par le pH du sol. Ces observations suggèrent que les traitements prélevant une large portion des éléments disponibles de la station tout en réduisant l'activité microbienne du sol pourraient limiter le développement du peuplement.
[Traduit par la revue]

Introduction

Microorganisms of a forest soil are largely responsible for its relative quality within limitations of climate, soil, and geology (Harvey, Jurgensen *et al.* 1980) and, thus, play a major role in forest soil productivity (Parkinson 1979; Fellin 1980; Harvey, Larsen *et al.* 1980; Jurgensen *et al.* 1980; Larsen *et al.* 1980; Mroz *et al.* 1980). Microbes mediate decay processes, nitrogen conversions, and mycorrhizal activity, thereby affecting plant growth conditions (Harvey, Jurgensen *et al.* 1980). Soil microbes, which are dependent on organic matter for an energy source, transform nutrients bound in surface litter into forms available for plant uptake. Therefore, belowground nutrient availability depends largely on aboveground moisture, temperature, and organic matter conditions, which influence the activity of soil microbes. Harvesting can alter this microbial activity by changing the amount and type of organic matter, soil pH, soil temperature, and soil moisture (Harvey, Jurgensen *et al.* 1980) and may have far-reaching effects on nutrient availability and

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future site productivity. Reducing the amount and type of fungi, for instance, may hinder degradation of the more resistant woody components, limiting the availability of some nutrients, especially on nutrient-poor sites.

The objectives of this study were to determine how timber harvesting and site preparation alter the activity of soil microorganisms and affect the relative percentages of bacteria and fungi (bacterial/fungal ratios) in microbial biomass in the organic layer of a northern Rocky Mountain forest soil.

Materials and methods

Site

The study site, located in the Graves Creek drainage near Lolo Pass, Montana (sec. 15, SE 1/4, tp.39N, rge.15W, Boise Meridian), is at an elevation of 1025 m on a south aspect with a 4% slope. Annual precipitation is 99 cm, 55% of which occurs as snowfall. Annual snowpack depth ranges from 3 to 4 m. Mean annual air temperature is 5°C, with extremes of −37 to 33°C. Soil surface temperatures under the litter range from −13 to 34°C. Soil in this area is an Andic Cryochrept derived from granitic bedrock. Recent litter, overlying 2 cm of decomposed duff, averages 5–9 cm thick. The root zone is almost exclusively limited to a 30- to 35-cm ash cap; the ash is a sandy loam with high infiltration and percolation rates.

The site, classified as an *Abies lasiocarpa – Xerophyllum tenax* habitat type (Pfister *et al.* 1977), is dominated by 82-year-old *Pinus contorta* var. *latifolia* Engelm. with an average diameter at breast height (dbh) of 16–32 cm, average height of 7 m, and average sapwood width of 2 cm. Two 120-year-old *Larix occidentalis* Nutt. (dbh 50–60 cm) and a few 1- to 6-year-old *Pseudotsuga menziesii* (Mirb.) Franco and *Abies lasiocarpa* (Hook) Nutt. also occur on the site. The sparse ground vegetation was composed mainly of *Arctostaphylos ura-ursi* (L.) Spreng. (39%), *Calamagrostis rubescens* Buckl. (7%), *Ledum glandulosum* Nutt. (10%), *Xerophyllum tenax* (Pursh) Nutt. (10%), *Vaccinium caespitosum* Michx. (5%), and *Vaccinium scoparium* Liebers (4%). Bare ground constituted 25% of the surface area.

Treatments

Four harvesting treatments, each applied to one 40 by 40 m plot, were implemented in August 1981 (Table 1); RL, clear-cut, only stems removed by hand, organic residue left; RR, clear-cut, whole trees (needles, branches, stems) harvested and removed by hand; RB, clear-cut, only stems removed by hand, organic residue broadcast burned (RB) at surface temperatures of 300–500°C; C, uncut control (C). Soil surface temperatures of the RB treatment were estimated from changes in color and degree of glossiness of glaze on ceramic plates. After harvest, the average thickness of the organic layer was 27 ± 7.2 cm for the RL treatment, 10.7 ± 4.7 cm for RR, 1.7 ± 0.4 cm for RB, and 12.5 ± 5.3 cm for C.

Soil sampling, testing, and analysis

We collected 20 random soil samples per plot from the organic layer midmonth from February 1982 (about 6 months after treatment) through January 1984 and used these samples to estimate microbial biomass and bacterial/fungal ratios in microbial biomass. Temperature of organic soil was recorded at five different randomly selected places immediately before sampling. Samples were then put in labeled plastic bags that were air and moisture tight and transported to the University of Idaho Forest Resources Laboratory. Soil pH was determined from a 1:1 paste of soil and water with a digital pH meter. Soil moisture was determined gravimetrically. Samples were held in the laboratory under moisture conditions similar to those found in the field at a temperature of 4°C and prepared for microbial testing within 10 days; this method does not significantly alter microbial activity (Ross *et al.* 1980).

Microbial biomass was determined by Jenkinson and Powlson's (1976) fumigation method, as modified by Lynch and Panting (1981). All visible roots were removed from the equivalent of approximately 20 g of dry organic soil. Each 20-g sample was placed in a 230-mL container and those containers were put in a 30-cm^3 desiccator along with a beaker of 60 mL of alcohol-free chloroform. Alcohol had been removed from reagent-grade chloroform by shaking 3 times with 5% concentrated H_2SO_4 in a separatory funnel. The chloroform was then washed 5 times with water and distilled in a rotary evaporator; the first 50 mL of distillate was discarded. The alcohol-free chloroform was stored over K_2CO_3 in the dark.

TABLE 1. Percent of organic residue removed during harvest (values in parentheses) or on the ground immediately after harvesting treatments, calculated from whole-tree measurements (100% cruise of 0.05 ha) according to Brown's (1977) method for predicting slash weight

Organic residue	Treatment			
	RL	RR	RB	C*
Litter	26	25	Ash	27
Ground vegetation	0.03	0.03	Ash	0.03
Needles	21	(20)	Ash	20
Branches (diameter < 0–7.6 cm)	13	(15)	Ash	12
Stems (diameter > 7.6 cm)	(40)	(40)	(40)	40
Cones	0.01	0.01	Ash	0.01
Lichens	0.02	0.01	Ash	0.02

*Only litter was on the ground; all other organic matter was tied up as perennial vegetation and, therefore, was unavailable to soil microorganisms.

The desiccator was evacuated until the chloroform boiled vigorously. The first two vacuums were held for 10 min; the third vacuum was held for 24 h at 23°C in the dark, after which the desiccator was evacuated 6 times, 30 min per vacuum, to remove the chloroform. After chloroform evacuation, the samples were removed and placed in 1.89-L jars, each equipped with a vial containing 10 mL of distilled water to maintain the moisture level and a vial containing 20 mL of 1 *M* NaOH to trap CO_2. Reinoculation with unchloroformed soil was not necessary. The jars were sealed and incubated at 23°C for 10 days. Samples were removed and oven-dried at 85°C for 24 h so that moisture content could be determined. One millilitre of 0.3 kg/kg $BaCl_2$ and four drops of phenolphthalein were added to the NaOH as a pH indicator and the solution was titrated with 1 *M* HCl.

Microbial biomass was then calculated according to Lynch and Panting's (1981) equation, $B = 0.673X - 3.53$, where B is microbial biomass in milligrams of carbon per 100 g of organic matter, 0.673 is the fraction of fumigated organisms mineralized to CO_2, and X is the amount of CO_2 in milligrams evolved per 100 g of fumigated organic soil. Jenkinson and Powlson's (1976) equation calculates biomass as $(X - x)/K$, where X is the CO_2 produced from fumigated samples, x is the CO_2 produced from unfumigated samples, and K is 0.45. Because Lynch and Panting's (1981) method and Jenkinson and Powlson's (1976) method were correlated, we were able to avoid the need to measure CO_2 production from unfumigated samples.

Bacterial and fungal contributions to respiration were determined with selective inhibitors (Anderson and Domsch 1975). Ten replicates of soil from each harvesting treatment were analyzed every other month. The equivalent of 50 g of dry organic soil was put in each of four 0.5-L plastic containers, each having a vial with 10 mL of 1 *M* NaOH to trap CO_2; four containers were used per replicate. One container had 150 mL of water and 6000 ppm glucose for estimating total respiration; the second, 150 mL water, 6000 ppm glucose, and 4000 ppm streptomycin (to inhibit bacteria); the third, 150 mL water, 6000 ppm glucose, and 2000 ppm cyclohexamide (to inhibit fungi); the fourth, 150 mL water, 6000 ppm glucose, 4000 ppm streptomycin, and 2000 ppm cyclohexamide. The inhibitor concentrations were the same regardless of season. The samples were incubated at 22°C for 8 h and readings taken by titrating the NaOH every 2 h. Milligrams of CO_2 per hour per kilogram of organic soil were plotted over time, producing four curves: (*A*) total repiration, (*B*) fungal respiration, (*C*) bacterial respiration, and (*D*) respiration of those microbes unaffected by streptomycin or cyclohexamide. Bacterial and fungal respiration was defined by $A - D$, bacterial respiration by $A - B$, and fungal respiration by $A - C$. Therefore, the percentage of bacterial activity is $100(A - B)/(A - D)$; the percentage of fungal activity is $100(A - C)/(A - D)$.

TABLE 2. Seasonal temperature (°C), moisture (kg soil water/kg dry soil), and pH data (mean ± SD) for the four harvesting treatments, by season, over the sampling period

	1982				1983				1984
Treatment*	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
				Temperature					
RL	1.5±0.5	12.0±2.0	16.0±3.0	10.8±2.0	1.2±0.1	13.2±3.0	16.3±5.7	10.2±7.6	1.2±0.1
RR	0.3±0.5	14.5±3.2	20.1±3.2	11.5±3.2	0.6±0.6	16.3±5.3	20.1±3.2	21.2±7.6	0.3±0.5
RB	0.3±0.5	15.1±2.7	27.3±6.3	13.8±4.2	0.3±0.5	17.8±4.8	27.0±4.3	22.7±5.7	0.3±0.5
C	0.3±0.3	12.0±3.1	17.2±3.5	10.7±4.7	0.3±0.5	15.3±2.7	18.3±4.6	12.6±4.8	0.2±0.3
				Moisture					
RL	2.08±0.73	1.90±0.42	1.26±0.45	2.11±0.56	2.18±0.102	1.67±0.29	1.24±0.28	2.04±0.46	2.20±0.48
RR	1.52±0.63	1.41±0.37	0.49±0.09	1.37±0.32	1.98±0.85	0.85±0.22	2.2±0.11	1.22±0.25	1.48±0.36
RB	1.42±0.28	1.23±0.38	0.10±0.14	1.26±0.43	1.94±0.52	0.88±0.13	2.7±0.12	1.06±0.26	1.46±0.42
C	1.46±0.38	1.60±0.28	0.81±0.21	1.46±0.42	1.96±0.62	0.85±0.25	4.1±0.25	1.33±0.23	1.36±0.27
				pH					
RL	5.9	6.0	5.9	5.9	5.8	5.9	6.6	5.9	6.0
RR	5.4	5.4	5.3	5.4	5.5	5.4	5.4	5.4	5.5
RB	6.0	6.0	6.0	6.1	6.4	6.0	6.1	6.0	6.0
C	5.6	5.6	5.6	5.6	5.3	5.6	5.6	5.6	5.6

*RL, clear-cut, residue left; RR, clear-cut, residue removed; RB, clear-cut, residue burned; C, uncut control.

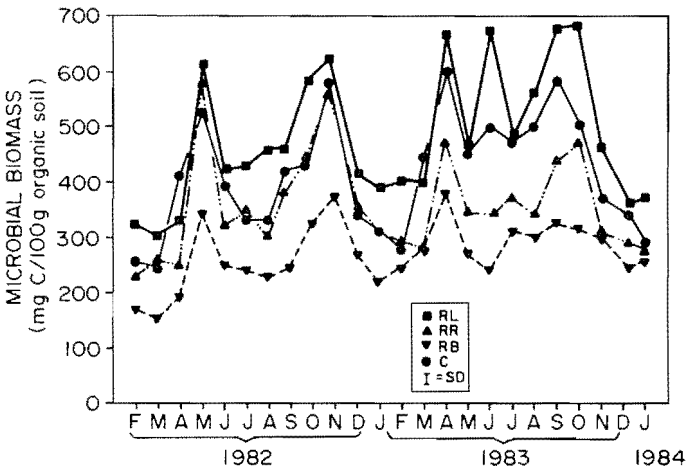

FIG. 1. Total microbial biomass in organic soil from the four harvesting treatments: RL, clear-cut, residue left; RR, clear-cut, residue removed; RB, clear-cut, residue burned; C, uncut control. Each data point is the mean of 20 replicates.

Statistical analysis

Data were subjected to a one-way analysis of variance (ANOVA) for a completely randomized design (Kirk 1982). SAS programs (SAS Institute Inc. 1982) were used to calculate the ANOVAs and regressions. Significance was determined at $p < 0.05$ with Fisher's protected least significant difference (LSD) test.

Results and discussion

Microbial biomass in soil from the C, RR, and RL treatments did not differ significantly ($p > 0.05$) during peak periods (Fig. 1); however, biomass in the RB treatment was significantly less than that from any of the other three treatments. Microbial biomass was greatest in the RL treatment, partly because of the large amount of easily degradable organic matter remaining after harvest. Temperature and moisture varied least in soil from this treatment (Table 2), probably because the harvest residue insulated the organic layer from freezing in winter and drying in summer, in both cases promoting biomass production. Microbial biomass in soil from the C treatment began increasing 1 month earlier than that in soil from any other treatment, presumably because the snow melted earlier in the control plot in both years, creating warmer soil conditions favoring microbial growth. Similarly, heavy rains and warmer soil temperatures caused microbial biomass to peak in soil from the RL and C treatments during June 1983. Soil from the RR and RB treatments may not have had enough degradable organic matter to respond to increased soil moisture as did the RL and C treatments; moreover, moisture and temperature in soil from the RR and RB treatments varied greatly throughout the sampling period.

When analyzed by treatment over season (Table 3), microbial biomass was significantly ($p < 0.05$) less in winter than in spring and fall, less in winter than in summer (but not significantly so), less in summer than in spring or fall (but usually not significantly so), and less in spring than in fall (but seldom significantly so).

Regardless of treatment, microbial biomass correlated positively ($R^2 = 0.86$) with soil moisture and negatively ($R^2 = 0.66$) with soil temperature during periods without snow cover. A three-dimensional diagram shows the relationship among soil microbial biomass and soil moisure and temperature (Fig. 2). Other researchers (Clarholm and Rosswall 1980; Kauri 1982; Lundgren 1982; Tewary *et al.* 1982; Boddy 1983; Orchard and Cook 1983) have reported similar results in unfrozen soil. Spring and fall biomass peaks in all treatments coincided with periods of high soil moisture; this supports the findings of Soderstrom (1979), Baath (1980), Clarholm and Rosswall (1980), Lundgren (1982), and Hunt and Fogel (1983). When soils were under snow, however, microbial biomass levels correlated positively ($R^2 = 0.62$) with soil temperature (Fig. 3).

Organic soil temperatures in northern Rocky Mountain forests usually are low (4–15°C) during periods of high soil moisture. Baath and Soderstrom (1982) reported that tempera-

TABLE 3. Microbial biomass (mg C/100 g organic matter; mean ± SE) by harvesting treatment over the sampling period

Year season	Treatment*			
	RL	RR	RB	C
1982				
Winter	319±31*a*	247±31*a*	172±24*a*	304±29*a*
Spring	515±42*b*	443±33*b*	302±41*b*	461±29*b*
Summer	430±36*a*	343±37*c*	241±29*c*	420±47*b*
Fall	551±52*bc*	502±36*d*	337±23*b*	522±68*c*
1983				
Winter	400±45*ac*	309±30*ac*	248±36*c*	297±42*a*
Spring	561±59*b*	409±64*b*	310±59*b*	501±52*c*
Summer	574±83*b*	320±41*ac*	284±41*b*	490±50*bc*
Fall	679±90*d*	448±39*b*	321±29*b*	534±64*c*
1984				
Winter	391±38*c*	289±27*a*	271±23*cd*	334±36*a*

NOTE: In each column, values followed by the same letter are not significantly different ($p < 0.05$) as determined by Fishers' protected LSD.

*RL, clear-cut, residue left; RR, clear-cut, residue removed; RB, clear-cut, residue burned; C, uncut control.

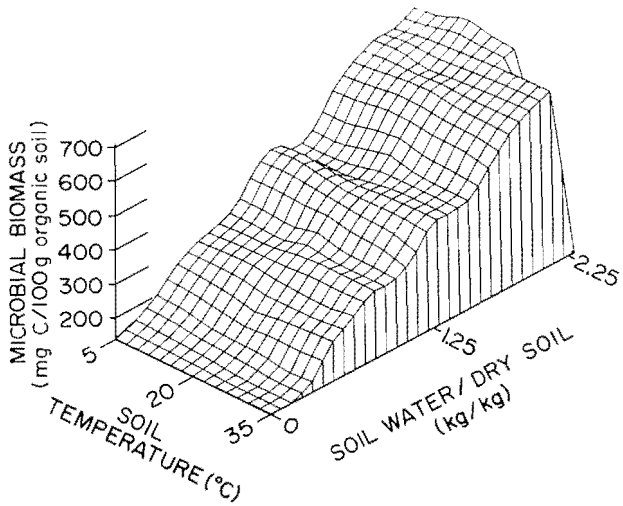

FIG. 2. Microbial biomass in organic soil in relation to soil moisture and temperature; data are pooled from all harvesting treatments.

ture varied inversely with soil water content in a *Pinus sylvestris* L. forest soil in central Sweden. Soil humus temperatures become warmer as soil moisture evaporates. In the northern Rocky Mountains, if soil temperature is above 5°C, soil moisture overrides the importance of soil temperature in affecting soil microbial biomass. During summer rains, microbial biomass can peak for short periods as a response to increased soil moisture. However, biomass is not significantly greater than that which routinely occurs in spring or fall. When easily degradable organic matter is adequate and increasing soil temperatures are accompanied by high soil moisture, microbial activity often levels off or decreases, possibly because the rate of O_2 diffusion declines to a level insufficient for maintaining increasing microbial respiration (Boddy 1983).

Microbial biomass estimates obtained by Lynch and Panting's (1981) method correlated posiively ($R^2 = 0.66$) with those obtained by Jenkinson and Powlson's (1976). The Lynch and Panting (1981) estimates are similar to those reported by Soderstrom (1979), Baath (1980), Sparling *et al.* (1981), and

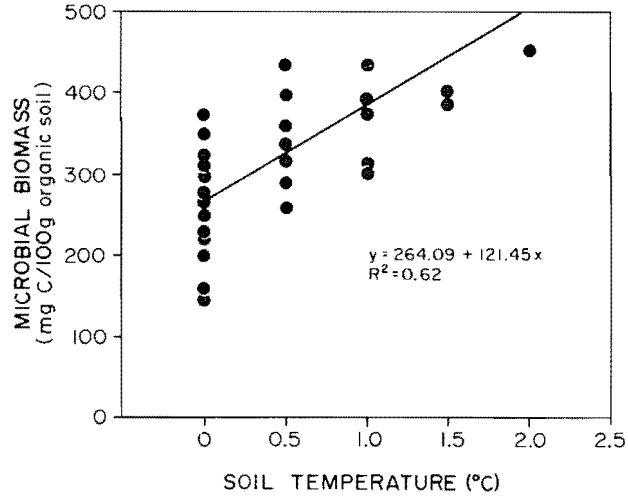

FIG. 3. Correlation of microbial biomass in organic soil to soil temperature during periods with snow cover at <3°C ($n = 56$, $p < 0.01$).

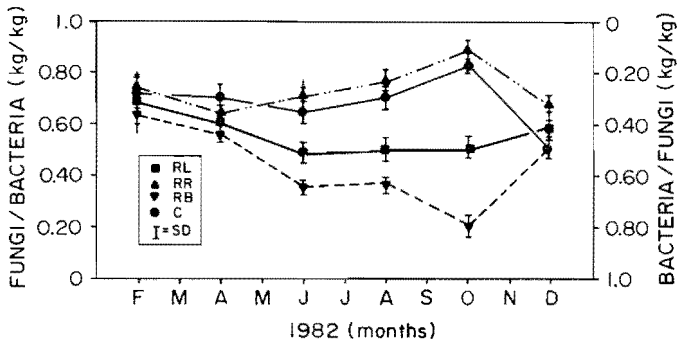

FIG. 4. Bacterial and fungal ratios in microbial biomass in organic soil from the four harvesting treatments in 1982: RL, clear-cut, residue left; RR, clear-cut, residue removed; RB, clear-cut, residue burned; C, uncut control. Each data point is the mean of 10 replicates.

Voroney and Paul (1984). The Jenkinson and Powlson (1976) estimates are similar to those reported in Jenkinson and Powlson (1980).

During periods without snow cover, soil from the C and RR treatments had relatively low bacterial percentages in microbial biomass and soil from the RB and RL treatments had significantly higher bacterial percentages than soil from C (Fig. 4) or than have been reported by Anderson and Domsch (1973, 1975). Under optimum conditions, bacteria grow and reproduce much faster than fungi. It is likely that optimum temperature and moisture conditions coupled with substantial amounts of organic residue (relatively low carbon/nitrogen ratio, high pH) in the RL treatment and nutrient-rich ash (Stark 1979) in the RB treatment (Renbuss *et al.* 1973; Widden and Parkinson 1975; Bisset and Parkinson 1980) gave bacteria a large competitive advantage. During periods with snow cover, bacterial and fungal percentages were roughly equal (ranging from 0.50:0.50 to 0.60:0.40); the previously high bacterial percentages in soil from the RB and RL treatments declined and the previously low bacterial percentages in soil from the C and RR treatments increased (Fig. 4). The pH of the organic horizon remained relatively constant throughout the sampling period regardless of treatment (Table 2). During periods without snow cover, bacterial and fungal percentages correlated positively ($R^2 = 0.79$) with soil pH regardless of treatment (Fig. 5); during

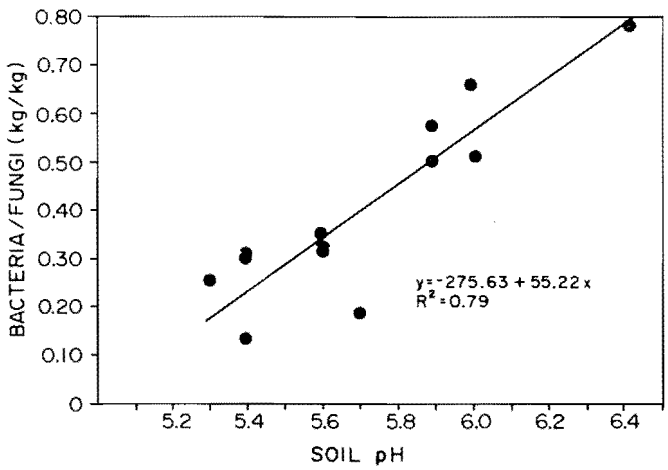

FIG. 5. Correlation of bacterial/fungal ratios of microbial biomass in organic soil to soil pH over all four harvesting treatments during periods without snow cover ($p < 0.05$). Each data point is the mean of 10 replicates.

periods with snow cover, bacterial and fungal percentages seemed unaffected by soil pH.

Timber harvesting drastically alters the organic layer of the soil, causing the bacterial/fungal ratios in soil microbial biomass to fluctuate. For instance, Lundgren (1982) found that bacterial biomass increased markedly within 2 years of harvest in a clear-cut area compared with that in a mature pine stand. Niemela and Sundman (1977) and Sundman *et al.* (1978) found that differences between bacterial populations of clear-cut and undisturbed sites were maximum approximately 7 years after clear-cutting and that bacterial populations of cut sites did not approach those of undisturbed sites until about 13 years after clear-cutting.

Changes in soil microbial activity brought about by timber harvesting would be expected to persist as along as changes in the abiotic variables and easily degradable organic matter that contribute to microbial metabolism persist. We do not intend to extrapolate the data from this case study beyond the limitations of this site. However, our study suggests that timber harvesting can affect microbial biomass and its bacterial/fungal ratios depending on the type of harvesting and site-preparation methods employed. When residue is left on site after clear-cutting, microbial activity can be expected to increase; when residue is removed or the site is broadcast burned, microbial activity can be expected to decrease. Clear-cutting and then either broadcast burning or leaving residue will most likely increase the bacterial percentage of microbial biomass, whereas clear-cutting and removing residue should not alter the bacterial/fungal ratios compared with those of an uncut stand.

Future tree growth after harvest will ultimately depend on mineralization of those nutrients from organic matter by soil microorganisms. Treatments such as the RR and RB, which remove a large portion of available nutrients from the site while reducing microbial activity, could eventually limit stand development. Clearly, more research is necessary before the full effect of site preparation on soil microbial biomass can be established.

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